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Pongo pygmaeus. By Colin P. Groves

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Pongo Lacépède, 1799

Orang utan (Malay), Mias (Dayak)

Pongo Lacépède, 1799:4. Type species *Pongo borneo* Lacépède, by monotypy.

Ourangus Zimmerman, 1777:399. Type species *Ourangus outangus* Zimmerman, 1777:399, by monotypy. Name invalidated by Opinion 257 of the International Commission for Zoological Nomenclature.

CONTEXT AND CONTENT. Order Primates, Suborder Anthropoidea, Superfamily Hominoidea, Family Pongidae. This family includes living genera *Pan, Gorilla,* and perhaps *Hylobates* as well as *Pongo. Pongo* includes one species as treated below.

Pongo pygmaeus (Hoppius, 1763)

Simia pygmaeus Hoppius, 1763:68. Type locality erroneously supposed to be Africa. Elliot, 1913:188, suggested that the specimen of Edwards upon which Hoppius based *pygmaeus* probably came from Sumatra rather than Borneo, but Elliot used the name for the Bornean subspecies rather than the Sumatran subspecies, hence by implication restricting the type locality to Borneo, a useage that has prevailed since.

Simia satyrus Linnaeus, 1766:34 (not of 1758, = the chimpanzee).

Ourangus outangus Zimmerman, 1777:399. Type locality unclear.

Pongo borneo Lacépède, 1799:4. Type locality Borneo.

Simia Agrias Schreber, 1799:suppl. Type locality Borneo.

Pongo Wurmbii Tiedemann, 1808:329. Type locality Borneo.

Pongo Abelii Lesson, 1827:32. Name wrongly attributed to "Clarke" [= Clarke Abel], 1826, by Elliot (1913:189). Type locality Sumatra.

Simia Morio Owen, 1836:92. Type locality Borneo.

Pithecus bicolor I. Geoffroy, 1841:526. Type locality Sumatra.

Simia Gigantica Pearson, 1841:660. Type locality Sumatra.

Pithecus brookei Blyth, 1853:375. Type locality Sarawak.

Pithecus owenii Blyth, 1853:375. Type locality Sarawak.

Pithecus curtus Blyth, 1855:527. Type locality Sarawak.

Satyrus Knekias Meyer, 1856:282. Type locality Borneo.

Pithecus Wallichii Gray, 1870:8, allegedly of Blainville, 1818 (see remarks). Type locality Borneo.

Pithecus sumatranus Selenka, 1896:386. Type locality Sumatra.

Pongo pygmaeus: Rothschild, 1904:421. First use of combination.

Pithecus wallacei Elliot, 1913:193, allegedly of Blainville, 1839; 46; and not used by Selenka, 1896. Type locality Borneo.

CONTEXT AND CONTENT. Context as noted above. There has been considerable dispute over the number of geographic variants worthy of subspecific (formerly specific) status; latest assessments (Van Bemmel, 1969; Jones, 1969) recognize the following two living subspecies:

P. p. pygmaeus (Hoppius, 1760:69), see above (*borneo* Lacépède, *agrias* Schreber, *wurmbii* Tiedemann, *morio* Owen, *wallichii* Blainville, *brookei* Blyth, *owenii* Blyth, *curtus* Blyth, *knekias* Meyer, *landakkensis* Selenka, *batangtuensis* Selenka, *dadappensis* Selenka, *genepaiensis* Selenka, *skalauensis* Selenka, *tuakensis* Selenka, *rantaiensis* Selenka, and *ladakensis* Selenka are synonyms).

P. p. abelii (Lesson, 1827:32) see above (*bicolor* I. Geoffroy, *gigantica* Pearson, *sumatranus* Selenka, *deliensis* Selenka, and *abongensis* Selenka, are synonyms).

Of the two subspecies, *P. p. abelii* is larger and cinnamon (rather than maroon, Chasen, 1940); males of *abelii* have longer beard and moustache; females of *abelii* have beards; the face is flatter, more elongate, and O-shaped (rather than prognathous and 8-shaped); males develop cheek-pads beginning at 10 years of age and proceeding to 20th year (rather than years 8 to 15), pads are flat and covered with downy hair (rather than curving forward and being sparsely haired); tend to be more muscular or "linear" in build (rather than tending to obesity in captivity); throat sac smaller; face grey (rather than bluish around the eyes) (Van Bemmel, 1969; Jones, 1969); the brachial index (radial length × 100/humeral length) is less (95.9 ± 3.17 S.D., $n = 14$, rather than 100.7 ± 3.93 S.D., $n = 12$, J. R. Napier, unpublished data); braincase shorter, nuchal surface longer (author's unpublished data).

DIAGNOSIS. The following characters are diagnostic of both genus and species: hands and feet similar, hallux and pollex short, phalanges and metapodials curved; intermembral index ((length of humerus + length of radius) × 100/length of femur + length of tibia) 135 to 150; pelage long, loose, reddish; skin grey-black, roughly papillated; face sparsely haired with beard, moustache; enormous cheek-pads in adult males; pendulous gular sac in both sexes, larger in males; face concave, very prognathous; braincase high, rounded; supraorbital torus poorly developed; dentition i 2/2, c 1/1, p 2/2, m 3/3; inner upper incisors larger than outer, canine larger in males than in females, first of the lower premolars slightly larger in males, premolars and molars bunodont, all teeth somewhat crenulated on occlusal surface when unworn, especially conspicuous on premolars and molars.

GENERAL CHARACTERS. Ears are small, without lobes. Nose is small, without expanded alae. Arms are 200% of trunk length; legs are short, only 116% of trunk length; hands are long, 53% of trunk length; feet are 62% of trunk length (Schultz, 1968). Hallux (first toe) is more reduced than thumb and lacks the terminal phalanx in 75.5% of females and 46.3% of males (Tuttle and Rodgers, 1966). Head and body length averages 956 mm. for males and 776 mm. for females, standing height 1366 mm. for males and 1149 mm. for females (Lyon, 1908). Weight averages 75 kg. for males and 37 kg. for females; a record height is 1800 mm. (Schultz, 1968). Females retain the rounded skull and narrow face of juveniles; most adult males develop a sagittal crest, to which

FIGURE 1. Skull of young male *P. p. pygmaeus* in lateral view. Note the high placement of braincase in relation to facial part of skull. Duckworth Laboratory of Physical Anthropology, Cambridge Univ., no. Pr.51.0.1.

FIGURE 2. Skull of female in frontal view (no. Pr.51.0.4).

attach massive temporal muscles, and on the face a pair of large laterally projecting cheek-pads (flanges, "blinkers"), which are hard excrescences of connective tissue. Males also develop a long beard and moustache, and the gular sac found in all orangs from shortly after birth becomes enormous and dewlap-like.

DISTRIBUTION. In recent times, found only on the two island of Sumatra and Borneo. In Sumatra now restricted to Atjeh, northwest of the Wampu river (Carpenter, 1938). In Borneo, probably widespread though not certainly known from the south; in Sarawak it still occurs along the Sadong and Butang Lupar rivers, south of Rejang, and near the headwaters of the Baram and Balui rivers. In Sabah, still tolerably frequent in Sandakan district. In June, 1964, 3800 were estimated to exist in the wild: Sabah 2000, Sarawak 700, Kalimantan 1000, Sumatra 100 (IUCN, 1966; Napier and Napier, 1967).

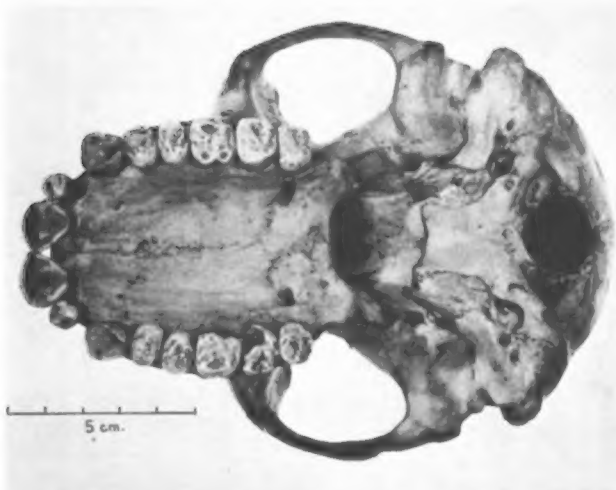

FIGURE 3. Palatal view of skull of young female. Note the wrinkled, bunodont molars and extreme incisor heteromorphy.

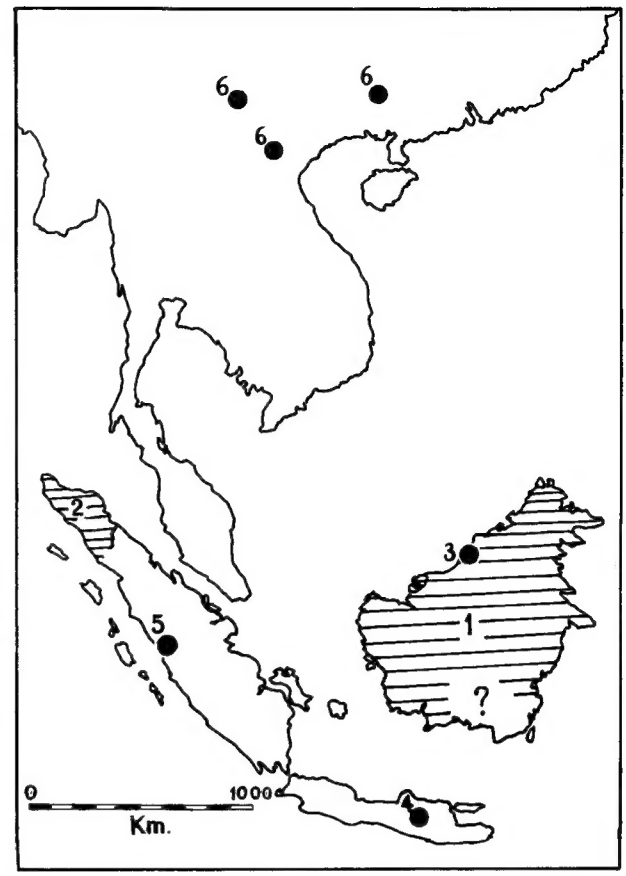

FIGURE 4. Map of part of southeastern Asia to show past and present distribution of *Pongo pygmaeus*. Numbers indicate: 1, Recent distribution of *P. p. pygmaeus* (present position is not definitely known either in Kalimantan or Sarawak); 2, *P. p. abelii*; 3, Niah Cave (Upper Pleistocene to Recent); 4, Trinil, Java (Middle Pleistocene); 5, Padang highlands, *P. p. palaeosumatrensis* (subfossil); 6, Kwangsi caves, Hoshangtun (Yunnan) and Tam-Hang and Tam P'a-Lui caves, N. Vietnam, *P. p. weidenreichi* (Middle Pleistocene).

Coolidge (1940) records a sighting of an orang at 6000 ft. (1850 m.) in Sabah, but states such an altitude is rare; Guan anak Sureng (1961) records a pair at 4800 ft. (1470 m.). Carpenter (1938) indicates orangs are not found in high central districts of Atjeh, above 1500 m.

FOSSIL RECORD. Subfossil orangs are known from beyond the present range: *P. p. palaeosumatrensis* Hooijer 1948:187, from caves in Padang Highlands of Sumatra, had teeth 16% larger than recent orangs, with less reduced second incisors, larger canines and first lower premolars, and greater sexual dimorphism in size. Orangs of unknown systematic position are known from Niah caves, Sarawak, from 37,000 B.P. to present (Medway, 1966). Middle Pleistocene orang teeth from Trinil, Java, are not larger than those of living examples, but those from the middle Pleistocene of southern China, *P. p. weidenreichi* Hooijer, 1948:280 (from Hoshangtung Cave, Yunnan) are even larger than *palaeosumatrensis*. This latter race is now known also from Kwangsi, and from Tam-Hang and Tam P'a-Lui in North Vietnam (Simonetta, 1957).

Remane (1965) has noted some dental features of dryopithecine Pongids from the Lower Pliocene of the Siwalik Hills of northern India and Pakistan, which foreshadow some characteristics of orangs.

FORM. Pigment layer in hairs is wavy and irregular (Wood-Jones, 1929); hair density is about 160 per sq. cm. on vertex, 175 on back, 105 on chest (Schultz, 1968). Intensity of palmar dermatoglyphic pattern is 70% greater than plantar; plantar thenar pattern more intense than hypothenar, but in palm thenar and hypothenar are equal (Midlo and Cummins, 1942).

The skull is high, the frontals ascend steeply above orbits. Orbits are close together, usually higher than wide. Nasal bones are strongly reduced in 3% of skulls (Wegner, 1966). Mandible is deep, short. Biegert (1963) interprets the characteristic form of the orang skull as related to the hypertrophy of the laryngeal sacs. Cranial capacity averages 424 cc. (320 to 540) in males, 366 (276 to 494) in females. A lacrimoethmoid suture is always present in orbit (Schultz, 1968). Vertebrae number c 7, t 12, l 4, s 4–5, d 2–3. Thorax is broader than deep; scapula dorsally positioned. Brachial index noted above. Crural index (tibial length × 100/femoral length) averages 92 (85 to 94) (Napier and Napier, 1967). Limb skeleton resembles that of other pongids except as noted above and as follows: humerus commonly with supratrochlear foramen; femur normally lacking fossa for *ligamentum teres*; *os centrale* present in carpus, tending to fuse with scaphoid only in old age; calcaneum comparatively short; tarsus shorter than length of third metatarsal; total length of phalanges of middle toe is more than 75% of length of tarsus plus metatarsus (Schultz, 1969). Medial incisors are broad and spatulate, especially the uppers; lateral incisors are small and initially pointed. Canines are large, thick in male, smaller in female; premolars are bicuspid except the lower anterior which, especially in male, has reduced metaconid; molars are relatively flat. At least one extra (fourth) molar found in 25% of male and 14.5% of female skulls, and nearly 1½ times as common in lower than in upper jaw (Selenka, 1896).

The *flexor hallucis longus* is rudimentary or absent (Straus, 1942); thumb musculature is surprisingly complex, an additional pair of short flexors arise on base of first metacarpal and insert on base of terminal phalanx; a deep head of *flexor pollicis brevis* is present (Day and Napier, 1963).

Aortic arch gives rise to innominate and left subclavian arteries; innominate gives off left common carotid, then divides into right common carotid and right subclavian. This pattern occurs in 90% of orangs (Straus, 1936); the human pattern, in which three arteries arise from the aorta, occurs in only 10%, and in these the arteries are more crowded than in man. The subclavian arteries are much bigger than the common carotids.

A pair of laryngeal sacs may be unequal in size, especially in males, extend from mandible (with diverticula towards ears) to sternum (with diverticula to the axillae), and vary in size with age and sex, being greatest in old males (Miller, 1941; Guilloud and McClure, 1969). Lungs are not lobed, but have vestigial fissures.

Intestinal tract is long, 6.13 times the body length (Sonntag, 1924). According to Sonntag and to Straus (1936), the digestive tract resembles that of man except for the following: *valvulae conniventes* usually well developed, numerous; vermiform appendix very long, spiral in form, but becomes relatively shorter with age; stomach elongate.

FUNCTION. The wrist can be abducted slightly more than in other pongids and can be adducted much farther (98° on the average; Tuttle, 1969). The metacarpo-phalangeal joints of digits 2 through 5 can be extended only to a position 19° from straight.

Orangs exhibit good colour discrimination of blue, green, yellow, and red (Tigges, 1963); constantly chooses coloured blocks over grey—one animal showed significant preference for red over dark brown, and for yellow over orange (Tigges and Tigges, 1965).

Other aspects of physiology have not been adequately investigated.

ONTOGENY AND REPRODUCTION. Gestation varies from 233 to 263 days; foetal membranes weighed 285 g. in one instance, maximum diameter of placenta was 175 mm.; chorionic villi are finer and more delicate than in man; less syncytium, even in early stages of pregnancy, than in man or gorilla (Graham-Jones and Hill, 1962). Newborn infants weigh from 1420 to 2040 g., average 1720 (12 individuals; Seitz, 1969). Suckling occurs every 3 to 4 hours for about 4 minutes each time (Asano, 1967); soft food is taken from mother's lips at 4 months (Harrisson, 1961); weaning occurs at around three years (Harrisson, 1961; Chaffee, 1967). Permanent dentition is complete long before full epiphyseal closure (Schultz, 1968).

Ovulation typically occurs on 15th day of a 30-day cycle, with luteinizing hormone level of 1.2 to 3.6 μg (Blakley, 1969); but cycle may be as short as 25 days (Chaffee, 1967) or irregular, varying between 31 and 62 days (in a zoo animal: Asano, 1967).

No marked perigenital swelling during menstrual cycle in female; menstrual flow is comparatively slight, lasting 3 to 4 days (Chaffee, 1967; Asano, 1967). During pregnancy, mammae and genitalia of female undergo enlargement (Graham-Jones and Hill, 1962; Fox, 1929). Twins are born occasionally (Anon., 1968).

Earliest successful breeding recorded for a female is 7¾ years, 8 years for a male, but sexual maturity is postulated for both sexes at 6 to 7 years of age; full growth is completed at about that age in females, but not until the 10th year in males; size of cheek-pads and body weight continue to increase even after this. The longevity record (Jones, 1968) is 51 years—a pair then living in the Philadelphia Zoo and thought to have been born about 1919.

ECOLOGY. Predators unknown, except for man (see below, under discussion of conservation). Tigers exist in Atjeh, but are unlikely to be serious predators on an arboreal species; leopards are not known in either Borneo or Sumatra. The clouded leopard is known to prey on proboscis monkeys (Davis, 1962) and could possibly take young orang utans.

A malarial parasite of orangs, *Plasmodium pitheci*, is morphologically distinct from those of man and other apes; 19% of the genera of helminth parasites found in orangs and not occurring among hominoids in general are shared with man, 14% with chimpanzee (52% are shared between man and chimpanzee). Certain lice shared by man and chimpanzee have not been recorded in orang utan.

Chief competitor is man; both are exceedingly fond of Durian fruit, and are known to become aggressive when supply is threatened.

These apes are highly arboreal, rarely descend to ground, and may be found at all levels in trees. Typically they inhabit dipterocarp forest (Schaller, 1961; Yoshiba, 1964; Davenport, 1967); in Sarawak, also found in peatswamp forest (Schaller, 1961). Population density varies from 0.2 to 1.0 per square mile (Carpenter, 1938; Schaller, 1961; Yoshiba, 1964).

Movements are somewhat irregular, as they search for fresh fruiting trees, especially durian. In Sumatra, said to migrate over great stretches in search of concentrations of preferred fruit (Carpenter, 1938).

Orang utans are not territorial. Home range has not been estimated. Of old orangs, 13% have dental caries; 61% have abscesses; 34% have healed bone fractures (Schultz, 1956). Osteoarthritis was recorded by Schultz (1969:190). A skin disease with lesions resembling a form of Blastomycosis yielded to treatment with daily dose of 1,000 mg. Griseofulvin (Binkley, 1959). A case of appendicitis was cured by surgery, the inflamed organ was full of faecal stones (Vervat, 1961). Air-sac infection, probably due to faecal contact, has resulted in accumulation of up to 1,500 ml. of fluid and inflammation of submucosal tissue; not all treatments used resulted in successful cures (Guilloud and McClure, 1969).

Diet is mainly frugivorous (Schaller, 1961), but leaves, bark, buds, and flowers are also eaten. Animal protein is not eaten.

Conservation: Orangs do compete with man for favoured food items, especially durian fruit, but recent drastic reductions in population have been largely caused by methods of capture, high mortality of captured young, and much deforestation of habitat (especially in Sumatra). The orang utan is in danger of extinction in the wild. Recent estimated numbers are given above under Distribution. Harrisson (1963) initiated a program, not entirely successful, to reintroduce young orangs (legally confiscated from their captors) into the wild. It is now illegal in the U.S.A., United Kingdom, and Germany to offer orangs for sale without valid export licences from their country of origin (Jones, 1968); the government of Singapore has recently clamped down on the trade in orangs through its port. These measures, though welcome, do not prevent unscrupulous institutions from acquiring illegally exported animals. No measure can prevent extermination in the wild if deforestation continues to reduce the suitable habitat.

The first successful breeding of an orang utan in captivity was in Philadelphia in 1928 (Fox, 1929; Van Bemmel, 1963); 33 were born in captivity between 1959 and 1963; and more since then.

Orangs are most easily captured when young, by shooting the mother. Of course, the youngster is often too young to survive long. Harrisson (1962) conservatively estimates that to acquire one live young orang for a zoo, at least three others have been killed—two mothers shot to acquire two babies, one of which dies in transit.

BEHAVIOUR. Behaviour in the wild was described by Schaller (1961), Yoshiba (1964), and Davenport (1967) (see also Carpenter, 1938; Harrisson, 1961, 1962).

Two or more females, usually with infants, are associated

in the most stable social groups; subadults also tend to travel together. Groups of more than six are very rare. Adult males travel alone, from time to time joining a group of females and young temporarily. No aggression between males was recorded.

Copulation usually occurs with the partners front to front and hanging by the arms from a support (Fox, 1929; Van Bemmel, 1963; Graham-Jones and Hill, 1962); other methods have however been described: male may mount female quadrupedally from rear, and wrap arms around female's torso (Chaffee, 1967). Copulation is not necessarily confined to oestrus (Asano, 1967). While a female is on the move, her infant clings to her back or side; when female is at rest, it always hangs on her hip. Infant grips its mother's fur, intertwining its fingers, while she moves, and locks itself to its mother in similar fashion while sleeping. Infant screams loudly if it thinks it is being abandoned.

Daily and seasonal movement is largely sporadic.

Orangs are comparatively silent. Within the small social unit, communicative sounds are made by smacking of the lips. When frightened, an orang screams, with the lips funnel-shaped; at times, males utter a deep roar or boom with the laryngeal sacs inflated (Schlegel and Müller, 1839–44; Schaller, 1961). In frustration or anger, orangs grind their teeth (Schultz, 1969).

Various locomotor modes are employed: climbing, quadrupedal branch-walking or bipedal walking (grasping branches with all four extremities); brachiation is common only in young. No jumping seen. On the ground, they walk quadrupedally with hands clenched or flat, on sides—not soles—of feet (Tuttle, 1967), or walk bipedally. Carpenter and Durham (1969) gave a detailed account of suspensory postures and locomotion. They are unable to swim (Hornaday, 1885).

Food is plucked with one hand, usually between fingers and palm, since thumb is too short for efficient manipulation, and is held in one hand while feeding.

Occasional attacks on man reported (Yoshiba, 1964); usual method of defence is by dropping or throwing showers of branches onto terrestrial intruder (Schaller, 1961; Davenport, 1967).

Orangs build nests at night, always in trees, usually 40 to 60 feet above ground (Yoshiba, 1964; Davenport, 1967). Nests are simple, are made without much branch weaving (Hornaday, 1885), are rarely re-used, but may be by a female with infant (Guan anak Sureng, 1961). New nests are constructed almost every night. Nests constructed by young, apparently untaught, from 18 months (Harrisson, 1961). Orangs lie on side or back to sleep.

Youngsters play alone or together; exploratory behaviour, especially tactile exploration, is conspicuous during play. Neither young nor adults are as boisterous or volatile as chimpanzees, but seem more lethargic and more quickly lose juvenile emotional traits, becoming slow and deliberate.

Yerkes and Yerkes (1929) described orangs as possessing considerable behavioural adaptability, learning by imitation, trial and error, and "insight." They are less curious than chimpanzee; occasionally use implements; possess what Reynolds (1967) described as "a particular flair for mechanical contraptions." Tactile exploration predominates over visual; greater repertoire of response to unfamiliar objects than other apes (Parker, 1969).

GENETICS. Diploid chromosomes number 48; the fundamental number of arms is 72; 26 autosomes are metacentric, 20 are acrocentric (16 large, 4 small); the X chromosome is metacentric, the Y metacentric; acrocentrics bear satellites (Chiarelli, 1961; Hamerton *et al.*, 1963). Of 30 orangs tested, 94.5% were non-tasters of PTC (Chiarelli, 1963).

Human antigens of the ABO blood groups are present; among 73 orangs, 31 were A, 24 were B, 18 were AB. The B-complex probably contains antigens absent from human group B (Franks, 1963; Wiener *et al.*, 1963; Schmitt, 1962; Landsteiner, 1928). Secretor gene (ABH substances in saliva etc.) is present (Wiener *et al.*, 1963). Antigens of the M blood group, of the MN system, were present in 10 orangs tested, but not identical to human M (Schmitt, 1962; Moor-Jankowski *et al.*, 1964). Of the Rh group, D-like and c-like antigens occur (Schmitt *et al.*, 1963). Blood factor I absent, i present but poorly developed (Wiener *et al.*, 1965).

Haemoglobin A_2 present (Barnicot and Jolly, 1966). Starch-gel electrophoresis of serum proteins shows divergence from chimpanzee, gorilla and man greater than that between them (Goodman, 1963). Special study of serum albumin by micro-complement fixation supports this conclusion (Sarich, 1968). Electrophoresis of transferrins suggests presence of two co-dominant alleles; the faster-moving component occurred in 11 orangs, the slower in 7, both in 11, suggesting a frequency of the faster allele of 57%; there is also a faint, slightly diffuse, very fast-moving band. Transferrins contain 4 residues of sialic acid, as in man (Nute and Buettner-Janusch, 1968). Myoglobin composition is similar to that of man and chimpanzee (Nakagawa *et al.*, 1969).

REMARKS. Not all of the original works cited in the synonymies above were seen by the author. The nomenclature of the orang utan was remarkably confused until Stiles (1926) demonstrated that the correct name is *Pongo pygmaeus* (Hoppius, 1763). Even so, some workers refused to accept this conclusion, which was backed up by Opinion 114 of the International Commission (1929), and continued to use the previously current *Simia satyrus* (*e.g.* Chasen, 1940). The name *Pongo* Lacépède is derived from the name of a supposed Angolan giant ape described by Battell (1613), but founded upon actual orang utan specimens; while Hoppius's *Simia pygmaeus* was based on reports, but not actual specimens as far as is known, probably of actual orang utans. The orang had long been known from Borneo, through specimens brought to Europe by the Dutch East India company; specimens of any ape that was described and dissected tended therefore to be called "orang-outang" or a variant of that name: hence much of the confusion over the applicability of the Linnaean name *Simia satyrus*.

Blainville did not use the name *Wallichii* or *wallacei* in the papers cited here for 1818 and 1839. He did discuss the specimen obtained by "M. Wallich" (1818:312).

In Malay, *Orang* means "man," *utan* "wild." The common misspelling *Orang utang* means "man in debt" (Harrisson, 1962). Correctly, therefore, the name should be spelled (and pronounced) as above, preferably without a hyphen.

Reports (*e.g.* Heuvelmans, 1959) of "hairy bipeds" in Sumatra and Borneo, known as *sedapa* or *Orang pendek* ("little man"), seem to be based in part on sightings of orang utans and gibbons on the ground, and in part on imagination.

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